BURROWING BEHAVIOR OF DENTALIUM

P. DINAMANI

Oceanographic Laboratory, University of Kerala, Ernakulam 6, South India

In a recent paper on the habits of *Dentalium entalis*, Morton (1959) has remarked that apart from a paper by Yonge (1937) on the ciliary currents in the mantle cavity, little is known about the mode of life of the Scaphopoda. Morton's account deals mainly with the digestive organs, but he has also described feeding and burrowing habits in these animals. In an earlier paper on *D. conspicuum* (Dinamani, 1963), I have pointed out that the mode of feeding by means of the captacula is quite different from what has been suggested by Morton (1959). His account of burrowing deals with the part played by the foot in actual embedment of the animal in the substratum. However, observations on living material of *D. conspicuum* show that activities similar to burrowing are carried on by the animal even after embedment. This paper deals with some of these aspects of burrowing and indicates their possible significance to the feeding habits of the animal.

Living specimens of *Dentalium (Dentalium) conspicuum* Melvill were caught from 30 m. depth off Cochin, and kept in glass tanks filled partly with bottom mud, of sea water in the laboratory.

BURROWING

First stage

In whatever position the animal initially is, during burrowing it has a righting reflex which, when the animal assumes the normal position of rest, brings its dorsal (concave) side upwards (Morton, 1959). This could be clearly demonstrated when the animal is placed in a horizontal position on the surface of the mud with the ventral (convex) side facing away from the substratum. The animal plunges into the substrate in the same position, with the foot proceeding to dig almost at right angles to the body, and when the anterior one-third of the shell has penetrated, the animal goes through a slow twisting motion which brings the concave side up. While the animal performs this twist, it has penetrated further into the mud so that at the end of the twist nearly the whole animal has become embedded. The whole maneuver can be vividly pictured and recorded if a quantity of very fine mud is allowed to settle over the layer of bottom material in the tank before introducing the animal. Now, an animal placed in the tank in the above position leaves a clear trail on the surface of the mud (Fig. 1A). The apex of the shell describes an arc and makes a half turn as the animal twists through nearly 180°, and the direction of the twist and its extent are marked by the apex of the shell on the fine mud (Fig. 1 A and D, *t'*).

Second stage

While "reading" the trails left on the mud surface by a few specimens, another feature of burrowing became noticeable. In addition to the trail left by the body of the animal as it drags forward and digs into the substratum (t in Fig. 1 A) and at a distance nearly equal to its own length in front, a saucer-shaped area of loose sediment was observed (t'', Fig. 1 A). At first the significance of these markings was not understood, but it was being regularly observed wherever a *Dentalium* had burrowed. In order to verify whether the burrowing habits of the animal were the cause of these formations, a specimen was kept under close observation after its passage from the surface into the mud. Soon after it had embedded itself in the normal position, the surface of the mud showed faint hair-line cracks at a site approximately above the buried front part of the animal. These cracks widened slowly as mud particles around became displaced, and eventually a slight depression appeared on the surface, clearly indicating that the burrowing activity of the animal had brought on this effect. Animals introduced in glass troughs filled partly with coarse sand or gravel do not leave a clear trail, but if a layer of fine mud is first allowed to settle on the surface of such material, the burrowing activities become clearly evident.

The action of the foot was later closely followed in a number of animals placed close to the walls of the glass trough, where their activity was partially visible through the glass partition. After the animal embeds itself, the pointed tip of the foot slides into the substratum (Fig. 1 B) in a series of wave-like movements, and at the same time the whole foot is moved in an arc towards the animal. This has a raking action on the sediment, and the pedal lobes, which are held pressed against the sides of the foot during these movements, are now erected and swung back (Fig. 1 C). Particles of mud loosened by the foot in front are shovelled back by the pedal lobes, and soon a small space is cleared around the foot. During these movements mud particles trickle down into the space cleared by the foot, and hair-line cracks appear on the surface of the mud above. The animal shifts its position occasionally, partly drawing back or going forward, with the result that when a space has been cleared around the front end of the animal, the column of mud immediately above the foot has developed many cracks and interstices, and as a result becomes loose-textured. Water also trickles through the cracks into the area cleared by the animal, and the pedal lobes acting in this fluid medium have a kind of churning action on the sediment, and occasionally a small quantity of water and mud is forced out through the cracks. This action repeated many times results in a small depression at the surface, formed of loose sediment (Fig. 1 A and D, t''). Periodically the foot is fully retracted into the mantle cavity, and this takes place in a definite sequence. First, the tip of the foot contracts, while the pedal lobes are fully expanded and held closely appressed to the mantle fringe behind. Now, the mantle contracts around the foot in the form of a collar till the pedal lobes and the tip of the foot are withdrawn into the mantle cavity. This behavior has two advantages: no water or foreign matter is allowed to enter the mantle cavity, and the particles of mud adhering to the foot and the pedal lobes are also wiped free by the mantle fringe.

Discussion

Action similar to burrowing on the part of *Dentalium* after it has embedded itself in the substratum results in a loosening of the sediment in an area immediately in front of the animal. As the sediment is worked loose by the foot, cracks develop

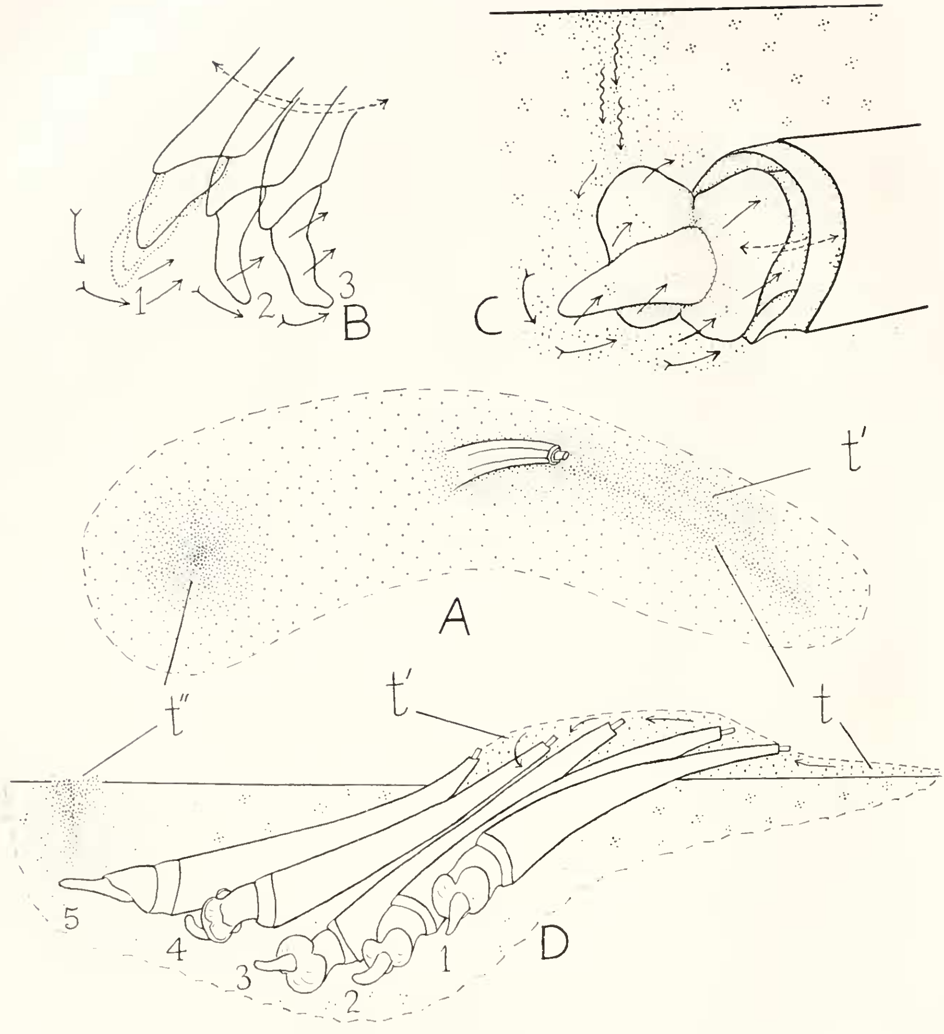

FIGURE 1. *Dentalium (Dentalium) conspicuum* Melvill. A. Markings made by the animal on the surface of the sediment as it drags itself forward (t), twists over (t') and embeds itself; t'' shows the loosened area of sediment above the front part of the animal. B. Movements of the foot as it slides into the substratum (shown by dotted outline) and is swung through an arc (indicated by dotted arrows). C. Wafting movements of the pedal lobes (indicated by dotted arrows) and the resulting shifting of sediment. D. Lateral view showing successive stages of the twisting motion (direction of twist indicated by arrows) which brings the concave dorsal side to the top at the end of burrowing, and the communication with the surface established through loosened sediment (t'') by the front part of the animal. In B and C, feathered arrows indicate direction of movement of foot and pedal lobes against the substratum, while unfeathered arrows indicate movement of sediment particles. In B and D, the sequence of events is indicated serially as 1, 2, 3. . . .

in the column of sediment lying immediately above and, aided by the continued wafting action of the pedal lobes, mud particles become displaced and begin to sink in from above. The net result is that a communication is soon established between the front end of the animal and the water column above through the intermediary of cracks and passages of the overlying sediment (Fig. 1 D). Water and sediment particles could then trickle down from above through the loosely-textured layer or be driven out due to the impelling action of the pedal lobes. It is suggested that this behavior of the animal may have an important functional basis: the loosening of the substratum by the foot and the pedal lobes results in a churning of the sediment that may help the animal to get at food particles among them with the captacula, the animal being entirely a deposit feeder. The sifting action becomes particularly important in capturing Foraminifera which occur in the deposit. These are generally considered to be the chief article of diet of *Dentalium* (Morton, 1959). The communication established through the overlying column of sediment may also help in drawing in particles of detritus from the surface. The stomach contents of the present species showed diatoms, single algal cells and unidentifiable detritus, and this could be available in quantities only from the surface deposits. It is also obvious that the captacula can seek for food only in a partly fluid medium, particularly since feeding is carried on through a ciliary tract in the captaculum (Dinamani, 1963). In those species living on sandy or gravelly bottoms, the interstices naturally occurring between particles of sediment may be sufficient to "ventilate" the stratum at the anterior end of the animal, though here, also, the burrowing action of the foot should have some effect.

The general view that connection between the scaphopod and the water column exists only through the posterior mantle tube can be held tenable if we take into consideration only the current of water going in and out of the mantle cavity for purposes of respiration, rejection of waste and extrusion of sexual products. This would fail to account for the important function of feeding, since the animal is a detritus feeder, feeding by means of the captacula. The captacula could obviously seek through the sediment for food only if the sediment is partially loosened. This is borne out by the fact that only after a period of digging among the sediments and the withdrawal of the foot do the captacula emerge for feeding (Morton, 1959; Dinamani, 1963). The behavior of the animal in establishing a communication with the exterior at the forward end may be for drawing in detritus matter from the surface deposits, and may therefore have an important bearing on nutrition. Periods of feeding and burrowing activities appear to succeed each other, and it would seem as if the animal's main burrowing activities are directed towards digging for food in the substratum.

Egg laying

On March 20, 1963, one of the specimens, measuring 65 mm. in length, soon after introduction into a larger trough of fresh sea water, laid a batch of eggs. The specimen, placed on the surface of the mud in an upside down position (with the ventral side up), remained at the surface for over 15 minutes. A small cloud was then observed issuing from the posterior aperture, being steadily impelled from the mantle cavity. It was deposited on the surface of the mud in the form of a long ribbon 6–7 cm. long. The ribbon consisted of small groups of 4 or 5 eggs each, barely touching each other, and a superficial count showed nearly 1000 eggs. The eggs were of a faint pinkish hue and measured 0.17 to 0.18 mm. in diameter, and had a clear membrane. The eggs were collected and introduced into a series of fingerbowls with fresh sea water, but because of high mortality, stages of development could not be followed closely.

Summary

Observations on living material of *Dentalium* (*Dentalium*) *conspicuum* Melvill show that after the animals have embedded themselves in the substratum, burrowing activities of the foot are directed towards loosening an area of the substratum around the foot. This causes sinking and displacement of material in the column of sediment overlying the foot, resulting in cracks and minute passages through which connection between the animal and the surface is established. The action of the foot and the pedal lobes in loosening and sifting sediment materials may enable the captacula to seek among them for food, such as Foraminifera and detritus. The connection established with the surface may also help in drawing in more detritus matter from the surface. The main digging activities of the animal appear to be directed towards seeking for food in the sediment. A note is also added on the mode of egg-laying observed in a single specimen.

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